

A CLOSER LOOK AT SOME MARINE HETEROTARDIGRADA

II. THE MORPHOLOGY AND TAXONOMY OF *BATHYECHINISCUS*, WITH A DESCRIPTION OF *B. CRATICULUS* N. SP. FROM THE CARIBBEAN

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ABSTRACT

Thulin's redesignation of specimens originally identified as *Bathyechiniscus tetronyx* as *Styraconyx sargassi* is shown to be in error. By possessing pedestalate bases to lateral cirri and clavae, these organisms fail to qualify for the generic distinction of *Styraconyx*. *S. sargassi* is therefore designated as a junior synonym of *B. tetronyx*. Since described features of *S. paulae* Robotti, 1971 did not differ significantly from those of *S. sargassi*, it is also designated a junior synonym of *B. tetronyx*. *B. craticulus* n. sp. is distinguished from *B. tetronyx* by its corrugated dorsal cuticle and the presence of a common sheath surrounding the clavae and lateral cephalic cirri. Since *S. hallasi* Kristensen, 1977 is more similar to *Bathyechiniscus* than to *Styraconyx*, it is reassigned as another species of *Bathyechiniscus*.

In 1926, Steiner with the Deutsch Sudpolar-Expedition, described *Bathyechiniscus tetronyx* from mud gathered at 385-m depth. Despite Steiner's stylized figures, Marcus (1936) and Mathews (1938) identified *B. tetronyx* specimens from *Sargassum* north of the Azores and from algae on the coast of California respectively. In 1942 Thulin erected the genus *Styraconyx*. Based on 45 specimens of the type species, *S. haploceros*, Thulin's detailed description emphasized, as the distinctive generic characteristic, that the posteriormost cephalic appendages arise rather far back along the side of the head and not from a raised "socket" or pedestal. The type species was further characterized by the absence of clavae and somatic cirri E and by the presence of short cephalic cirri. Thulin also contended that *B. tetronyx* reported earlier by Marcus was more similar to the new *Styraconyx* in that no supporting pedestal is shown for lateral cirri and clavae in the ventral illustration of Marcus (1936). Thus, in five lines and with no additional figure, Thulin established *S. sargassi* as an objective synonym for that specimen.

Rodriguez-Roda (1947; 1953) and Chitwood (1951) reported and figured specimens of *B. tetronyx*, either unaware of or ignoring Thulin. In calling attention to Thulin's work, Bois-Reymond Marcus (1952; 1960) indicated concurrence with Thulin's decision to switch the Marcus *B. tetronyx* to *S. sargassi*. She based her judgment on the form of the head, the position of the cephalic appendages, and on a correspondence between their specimen and Thulin's illustration of the feet and claws of *S. haploceros*. Her suggestion that earlier observations of Mathews, Rodriguez-Roda, and Chitwood should be designated as *S. sargassi* has been accepted since. Recent references to *S. sargassi* include Renaud-Mornant (1967; 1976) from the Pacific Ocean and Renaud-Mornant (1979) from the Indian Ocean.

Two additional species of *Styraconyx* have been described. Robotti (1971) used the presence of eyes and differences in the shape of clavae and fourth leg papilla/spines for his description of *S. paulae*. Kristensen (1977) designated *S. hallasi* on the basis of short clavae on a large pedestal, presence of small cephalic papillae, cephalic cirri with medial constrictions, and details of claws and toes.

During spring 1979, I collected specimens of the *Bathyechiniscus-Styraconyx* group from rinsings from the red alga, *Laurencia papillosa*, attached to beach rock at the head of a small cove at St. Croix, USVI. The opportunity to observe

these specimens using both Nomarski Differential Interference Contrast (DIC) and Scanning Electron Microscopy (SEM) revealed them to be a new species and provided the opportunity to reexamine this confused assemblage. Further collections along the north coast of Hispaniola in 1980 have provided additional specimens.

MATERIALS AND METHODS

Sand and algal samples were preserved in 5% formalin containing rose bengal stain, which made animals much easier to observe during subsequent procedures. An elutriation procedure was used to extract specimens. Animals were transferred to lens paper folded to line a perforated Beem Capsule by use of a 100- μ l automatic pipet. The entire capsule could be transferred with ease from vessel to vessel in the following fixation and dehydration series: overnight in 5% glutaraldehyde; 30-min periods in each of 50%, 70%, 95%, 100% and a second 100% ethanol. Full strength ethanol was also used as the transfer liquid, being replaced by liquid and then gaseous CO₂ in a critical point drying apparatus (Model E 3000, Polaron Equipment Ltd., Waterford, England). Individual specimens were removed from the lens tissue, using a hair as the transferring implement, and arranged on a piece of double-stick tape, tightly affixed to an aluminum SEM stub. Specimens were coated to approximately 200 Å with gold using a sputter coater (International Scientific Instruments, Model P-Si). Observations were made on a scanning electron microscope (ISI Model Super IIIA) at 10 kV, usually at a working distance of 8 mm. Nomarski Differential Interference Contrast observations (DIC) were made using an Olympus Vanox Research Microscope.

OBSERVATIONS

Genus *Bathyechiniscus* Steiner, 1926

Emended Diagnosis.—Cylindrical Halechiniscidae with four fully developed toes, each bearing claws with three or more vertically arrayed exposed points, on medial digits at least. Well-developed cephalic cirri present, including median cirrus. Single pair of clavae immediately adjacent to lateral cirri with one or both of these structures arising from a distinct lateral extension of the head, i.e., from a pedestal base. Spines present on legs I–III and papilla or papilla/spine combination on legs IV. Lateral folds of cuticle or alae absent.

Discussion.—Comparison between specimens to be described below and those previously described revealed an important error in the literature. Distinct pedestal bases are found on posteriormost cephalic appendages in St. Croix specimens, as well as those illustrated or described by Chitwood (1951), Rodriguez-Roda (1947; 1953), Renaud-Mornant (1967) and Kristensen (1977—at least for clavae). In fact, pedestals are suggested in figures of Marcus (1936). This is in direct conflict with the generic distinction for *Styraconyx* (Thulin, 1942). Thulin's misinterpretation of this feature may be explained by the fact that in ventral view, the pedestal bases of these dorsally located appendages can be obscured by the contour of the head. This relationship is observable in St. Croix specimens (Fig. 3A) and in ventral vs. dorsal illustrations of Chitwood (1951). Lacking the generic distinction of *Styraconyx*, these organisms (including all references to date, except Thulin's original description of *S. haploceros*) should be referred to the original generic name, *Bathyechiniscus*.

There remains some uncertainty regarding claw shape in *Bathyechiniscus*. Although Steiner described claws of *B. tetronyx* each with four exposed points, most others since reported three exposed points per claw. On the other hand, the claw itself is crescent-shaped and while the posteriormost tip of the crescent is actually embedded in toe tissue, it would be easy to interpret it as a fourth point. This is shown clearly by Chitwood (1951, fig. 1) who drew claws identical to those known to have three exposed tips but who interpreted them as four points. Additional

Table 1. Measurements (μm) of morphological characteristics of three life history stages of *Bathyechiniscus craticulus* n. sp. from St. Croix. Mean \pm 1 SD (range). n.d. = no data

Characteristic	Adults	Immatures	Juveniles
Body length	113.0 \pm 8.9 (101.4–124.8)	88.5 \pm 6.9 (78.0–95.6)	71.8
Median c. cirrus	8.2 \pm 1.1 (5.9–8.8)	7.7 \pm 0.6 (6.8–8.2)	4.7
Internal c. cirri	10.4 \pm 1.1 (9.8–13.1)	9.7 \pm 0.2 (9.4–9.8)	7.8
External c. cirri	8.8 \pm 1.7 (5.9–10.1)	8.0 \pm 1.3 (6.8–9.4)	7.8
Clava	9.3 \pm 0.7 (7.8–9.9)	8.1 \pm 0.9 (6.8–9.3)	7.0
Lateral c. cirri	19.9 \pm 1.2 (18.7–22.4)	15.8 \pm 1.4 (14.6–17.9)	15.6
Somatic cirri E	16.5 \pm 1.8 (14.6–17.6)	13.7 \pm 1.5 (11.7–15.6)	15.6
Leg I—spine	6.9 \pm 0.8 (5.9–7.8)	5.9 \pm n.d. (n.d.)	3.9
Leg II—spine	7.4 \pm 1.8 (5.9–9.8)	5.4 \pm 0.7 (4.9–5.9)	3.9
Leg III—spine	8.4 \pm 1.1 (7.8–9.8)	6.2 \pm 0.5 (5.9–6.8)	n.d.
Leg IV—spine/pap.	9.7 \pm 0.8 (8.6–11.7)	7.4 \pm 0.8 (6.8–8.6)	6.2
Bulb diameter	12.1 \pm 1.0 (10.9–13.7)	11.3 \pm 0.5 (10.8–11.7)	8.2
Number examined	10	5	1

testimony to the difficulty in discerning these fine features accurately can be found in Marcus's (1936) description showing two exposed points in his specimens—a feature modified later by Bois-Reymond Marcus (1952) to include three points. In any case, claw details of this sort would not be sufficient alone to justify generic distinction.

Type Species *B. tetronyx* Steiner, 1926

B. tetronyx Marcus, 1936; Mathews, 1938; Rodrigues-Roda, 1947, 1953; Chitwood, 1951.

Synonymy.—*S. sargassi* Thulin, 1942, and Bois-Reymond Marcus, 1952, 1960 (these three are references to the *B. tetronyx* of Marcus, 1936); Renaud-Mornant, 1967, 1976, 1979; *S. paulae* Robotti, 1971.

Emended Diagnosis.—*Bathyechiniscus* with clavae greater than $\frac{1}{3}$ length of lateral cirri. Clavae and lateral cirri separate and on common pedestalate base. Body contour smooth dorsally. Papilla/spine appendages on legs IV.

Discussion.—Minor variations in claval shape, leg IV appendage proportions, and relative size of the lateral cirri were used to distinguish *S. paulae* from *S. sargassi* (Robotti, 1971). Such features, especially as observed on a single specimen, are not considered of sufficient significance to justify the erection of a new species. The remaining distinctive characteristics of *S. paulae*, the presence of eyes, is known now to vary depending upon preparation of specimens. Renaud-Mornant, 1976 (corroborated in this study) pointed out that eyes obvious in live organisms may become entirely invisible in preserved ones. In the absence of additional specimens to reinforce distinctive characteristics of *S. paulae*, I believe that it must be treated as indistinguishable from *S. sargassi* and thus as a junior synonym of *B. tetronyx*.

Some uncertainty lingers with regard to the similarity of the type specimen and others subsequently designated as *B. tetronyx*. This is largely the result of Steiner's description of claws possessing four exposed points rather than the three points of subsequent descriptions. Reasons for this discrepancy have been discussed above. Kristensen (1977) raised the possibility that this grouping may be poly-specific especially on the basis of claval length. That decision will require further investigation.

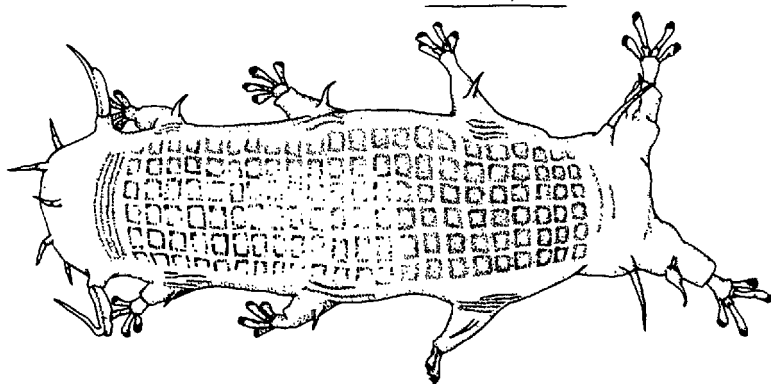


Figure 1. *Bathyechiniscus craticulus* n. sp. from St. Croix. Illustration from dorsal aspect. Marker = 25 μ m.

Additional Species *B. hallasi* (Kristensen, 1977)

Synonymy.—*Styraconyx hallasi* Kristensen, 1977.

Emended Diagnosis.—*Bathyechiniscus* with short clavae, less than $\frac{1}{3}$ length of lateral cirri. Clavae arise from individual pedestals, not shared with lateral cirri. Legs IV with papilla only.

Discussion.—Since *S. hallasi* fails to qualify for the genus *Styraconyx* because of the pedestalate base to its clavae, this organism is treated here as a second species of *Bathyechiniscus*.

Bathyechiniscus craticulus n. sp.

Diagnosis.—*Bathyechiniscus* with dorsal cuticle formed into distinctive grid-like pattern. Clavae and lateral cephalic cirri on common pedestalate bases and bound together by transparent sheath. Clavae about $\frac{1}{2}$ length of lateral cephalic cirri. Papilla/spine appendage on legs IV.

Etymology.—The specific name refers to the grid-like pattern of the dorsal cuticle: *craticulus* (L.), lattice comprised of an open structure of crossed strips.

Discussion.—While diagnostic features of this species are obvious using SEM, they are also generally visible using brightfield techniques. However, since no specific mention was made of the dorsal body contour by Steiner (1926), we must bear in mind that the original specimens of *B. tetronyx* may have possessed this feature as well. It is clear that other specimens described or figured since have not possessed such grid-work.

Type Specimen.—Adult, female (USNM No. 68683) collected March 1979, L. W. Pollock. In addition to the type specimen and 3 paratypes (USNM Nos. 68684–68686) deposited in the United States National Museum of Natural History, 13 additional paratypes are being held in the author's collection.

Distribution.—Type locality: Algal rinsings at Smuggler's Cove, east end of St. Croix, U.S. Virgin Islands (N 17°45'30"; W 64°35'36"); also found at: Point Fortaleza, Puerto Plata, Dominican Republic; Plage Cormier, northwest of Cap Haïtien, Republic of Haiti; Guadeloupe, West Indies.

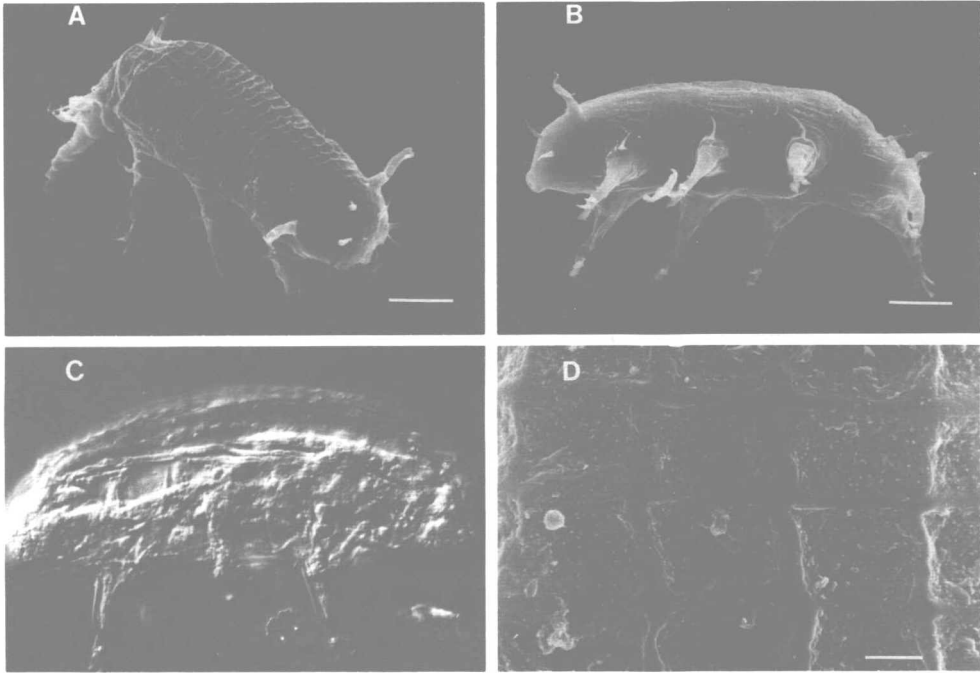


Figure 2. *Bathyechiniscus craticulus* n. sp. from St. Croix. A, dorsal view showing lattice pattern, marker = 20 μm ; B, lateral view of female, 760 \times , marker = 20 μm ; C, lateral view using Differential Interference Contrast to show dorsal corrugations under light microscopy; D, detail to show regularity of dorsal grid pattern, 6,700 \times , marker = 2 μm .

Description.—Treatment here is broad enough to include members of the type series. Parenthetical measurements are of the type specimen. Table 1 includes size data from three size groupings within the population from the type locality. Figures 1–3 show various aspects of the morphology of this new species.

Body cylindrical (111.2 μm in length). Posterior $\frac{1}{4}$ distinctly narrower than anterior $\frac{3}{4}$ (23.4 μm as opposed to 29.3 μm). Dorsal body contour with distinct grid-like pattern (Figs. 1, 2A). Twenty-three ribs traverse the dorsal surface at right angles to the long axis, beginning just behind the clavae and extending to 0.5 \times the distance between legs III and IV. From 5–7 equally spaced longitudinal ribs connect each pair of transverse ribs with the exception of the first pair. In addition 4–5 short parallel folds occur just above legs I–III, as shown in Figure 2B. Viewed laterally, the dorsal body contour appears ribbed or corrugated using brightfield microscopy, Figure 2C. In some preparations this dorsal mantle seems especially pronounced overlapping the bases of the leg pairs to some degree. While grid is absent ventrally, a fine punctuation or fields of shallow depressions is typical of the cuticle generally (Fig. 3A). At SEM magnification tears in the cuticle reveal supportive cuticular columns (Fig. 3D), which appear smaller but similar to those of *Batillipes* and *Echiniscus* (Schuster et al., 1975). Occasional irregularly spaced pores are found as well. While their function is unknown, similar pores have been described from *Batillipes* and *Pseudechiniscus* (Schuster et al., 1975). Somatic cirri E are prominent dorsolateral spines (156.6 μm) located above bases of legs IV.

A full set of cephalic cirri is present. The median cephalic cirrus (5.8 μm) is

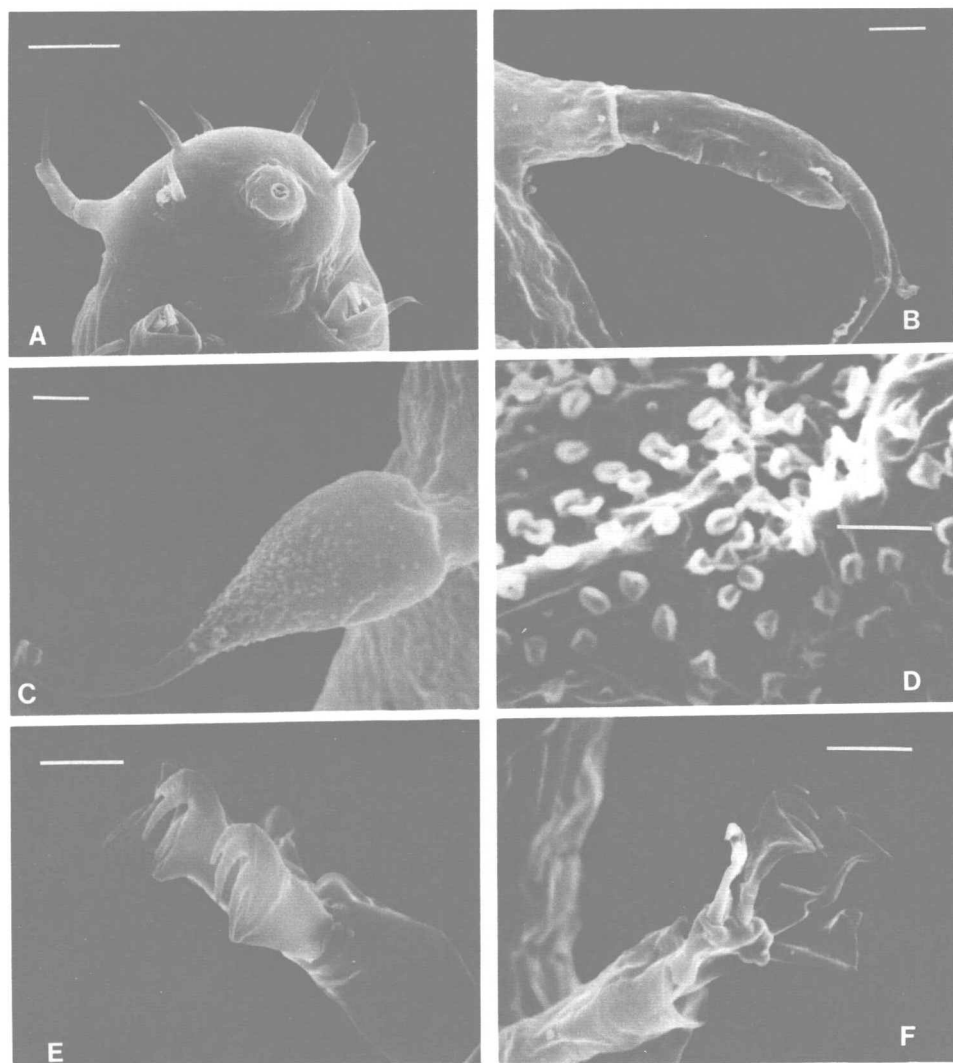


Figure 3. *Bathyechiniscus craticulus* n. sp. from St. Croix. A, head, ventral view, 2,150 \times , marker = 10 μ m; B, dorsal view of right clava and lateral cephalic cirrus to show common sheath, 7,100 \times , marker = 2 μ m; C, papilla/spine appendage from leg IV, 14,500 \times , marker = 2 μ m; D, supporting rods in torn cuticle, ventral surface, 21,600 \times , marker = 1 μ m; E, foot of leg I, right side, adult, 9,800 \times , marker = 2 μ m; F, foot of leg III, left side immature (note outermost toes with single pointed claws), 9,600 \times , marker = 2 μ m.

placed well back from the anterior margin of the head. Internal cephalic cirri (11.3 μ m) are dorsal and more medial than external cephalic cirri (8.6 μ m). Lateral cephalic cirri (19.5 μ m) and clavae (9.8 μ m) are located well back along the sides of the head. All cephalic cirri are divided by a medial constriction, as described for *B. hallasi* (Kristensen, 1977). While brightfield microscopy shows that the lateral cirri and clavae are entirely separate structures, the SEM, observing only surface features, reveals that they are bound by a common sheath, extending at least $\frac{2}{3}$ along the length of the clava (Figs. 3A, 3B), leaving only the claval tip

Table 2. Measurements (μm) of morphological characteristics of various *Bathyechiniscus* populations (n.d. = no data)

Characteristic	<i>B. craticulus</i> Cap Haïtien	<i>B. craticulus</i> Guadaloupe	<i>B. hallasi</i> Greenland	<i>B. tetronyx</i> Polynesia
Body length	118.6	148.2	139.5	157.3
Median c. cirri	9.4	9.5	7.5	9.3
Internal c. cirri	11.0	15.6	15.0	8.1
External c. cirri	9.2	10.1	12.0	11.8
Clava	9.4	8.6	7.5	9.8
Lateral c. cirri	18.7	23.4	42.0	22.3
Somatic cirri E	18.9	25.0	45.0	20.3
Leg I—spine	6.0	10.9	9.0	n.d.
Leg II—spine	6.3	n.d.	18.0	n.d.
Leg III—spine	6.0	8.8	20.0	n.d.
Leg IV—spine/papilla	9.4	12.5	6.0	n.d.
Bulb diameter	14.2	16.4	n.d.	n.d.
Number examined	4	1	n.d.	4
Source	present study	present study	Kristensen, 1977	Renaud-Mornant, 1976

free. In only two specimens of 22 observed did the common sheath appear to be lacking or disrupted. Accessory appendages are present on the shank of each leg. They appear as spines near the point of attachment of legs to the body or legs I ($5.9 \mu\text{m}$), legs II ($6.8 \mu\text{m}$), and legs III ($8.8 \mu\text{m}$). The prominent papilla/spine appendage of legs IV ($11.7 \mu\text{m}$) is in fact a single continuously tapering structure (Fig. 3C). The granular appearance of the middle portion of its surface is a consistent feature at the SEM level although its significance is unknown.

Legs and feet are telescopically retractile distally and claws can be withdrawn into membranous sheaths as described for *B. tetronyx* by others. The three points on each adult claw are progressively longer in the series: accessory spine, primary point, secondary point (Fig. 3E). While the accessory spine is smallest, it is not nearly as thin as that shown for *B. hallasi* (Kristensen, 1977). As in previous descriptions, the medial digits are longer than the lateral digits, and medial digits possess heart-shaped pads proximally (Fig. 3F), described as adhesive by Kristensen (1977). Prominent peduncles, visible using brightfield technique, are embedded within the lateral toes only. Juveniles lacking gonopores also lack accessory spines and secondary points on the lateral digits of each foot (Fig. 3F). This relationship has also been described for *B. hallasi* (Kristensen, 1977). A single juvenile specimen was observed in which lateral toes on each foot were entirely missing.

The only specimens oriented in such a way as to make their gonopores visible were females. The female gonopore consists of a set of six distinct cuticular folds. The anus is flanked by a pair of lateral cuticular folds, with a small triangular flap anteriorly. Such an arrangement has been described for *Stygarcus* (Pollock, 1970) and *Echiniscoides* (Kristensen and Hallas, 1980).

Discussion.—St. Croix specimens are most similar to *B. tetronyx* as figured in Marcus (1936) and Chitwood (1951). However, significant differences are found in the corrugated dorsal surface and the common sheath binding clavae and lateral cephalic cirri together. While both these features are far easier to observe using SEM, evidence of both is visible using conventional brightfield microscopy. The dorsal corrugations can be seen most clearly from the lateral perspective (Fig. 2C). Lateral illustrations of *B. tetronyx* show no such corrugations (Marcus, 1936;

Mathews, 1938; and Chitwood, 1951). While the common sheath, clearly seen with SEM, is not visible using brightfield microscopy, its presence is revealed by the permanent tight apposition of these two structures in *B. craticulus*. Clavae and lateral cephalic cirri of *B. tetronyx* are shown as clearly separated structures by Marcus (1936), Mathews (1938), and Robotti (1971).

Comparative data on various developmental stages of *Bathyechiniscus* populations appear in Tables 1 and 2. In Table 1, adult specimens have 4 toes per leg; each toe with 3 exposed points. Immature specimens lack gonopores and have four toes per leg, but outermost toes bear only one exposed point. Juveniles are those specimens bearing only two toes with three-pointed claws (i.e., the middle two toes of adults) per leg. Table 2 includes data on adult *B. craticulus* from Cap Haitien, Republic of Haiti, and from Guadeloupe (the latter, a single specimen generously provided from the collection of J. Renaud-Mornant). Also, data regarding closely related species are provided: adult *B. hallasi* from Godhavn, Greenland (from Kristensen, 1977) and adult *B. tetronyx* from Polynesia (from Renaud-Mornant, 1976). All possible paired combinations of these data were compared using techniques described by Pollock (1971) in order to discern points of major dissimilarity in measured characteristics, having adjusted for differences in overall sizes.

Comparisons among three populations of adult *B. craticulus* in the Caribbean showed no substantial differences. Points of major departure included measurements of leg appendages which, because of their orientation and size, are especially prone to observational error. Clavae in the Guadeloupe specimen are disproportionately smaller than those from St. Croix, although examination of additional specimens from Guadeloupe will be necessary to determine the significance of this feature.

B. craticulus differs in most important meristic features from *B. hallasi*. Median cirri, clavae, and especially the papilla/spine of leg IV are all much longer in *B. craticulus*. On the other hand, lateral cephalic cirri, somatic cirri E and spines on legs II and III are disproportionately longer on *B. hallasi*. Virtually all structures are disproportionately shorter in *B. tetronyx* from Polynesia. Such differences underscore the more fundamental distinctions among these three species based on features such as dorsal body contour and the shape of clavae and their pedistal bases.

Comparative length-corrected measurements from groups within a species can provide information regarding ontogenetic changes. *B. craticulus* adults and immature individuals (from St. Croix at least) possess approximately the same body and appendage proportions. While in most cases appendages are proportionately a bit longer in immature organisms, the differences are not substantial. Juveniles have disproportionately large external cephalic cirri and somatic cirri E in comparison to adults, although the significance of these features is unknown.

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